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MORPHOLOGICAL FEATURES OF FUNCTIONAL SIGNIFICANCE IN THE GILLS OF THE SPINY DOGFISH, *SQUALUS ACANTHIAS*

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A great many studies have now been made concerning the physiology of the gills of the spiny dogfish, *Squalus acanthias*. In addition work has been published under the names *Squalus suckleyi*, *Squalus lebruni* and *Acanthias vulgaris*, all of which are probably synonymous with *Squalus acanthias* (Bigelow and Schroeder, 1948).

Papers have dealt with the flow of water through the branchial chamber (Balabai, 1939; Lenfant and Johansen, 1966), the fall in blood pressure across the gills (Burger and Bradley, 1951), the persistence of the pulse wave into the dorsal aorta (Sheldon, Sheldon and Sheldon, 1962). Study of the exchange of materials between blood and water includes urea (Smith, 1929; Boylan, 1967; Goldstein and Forster, 1962); thiourea (Boylan, 1967); water (Smith, 1931; Boylan, Johnson and Antkowiak, 1962); Na^{22} (Burger and Tosteson, 1966; Horowicz and Burger, 1968); O_2, CO_2, bicarbonate and lactate (Robin, Murdaugh and Millen, 1966; Murdaugh and Robin, 1967); maintenance of osmotic status (Boylan, Kim, Farber and Gerstein, 1965); various organic compounds (Rall, Bachur and Ratner, 1966); and various drugs (Maren, Embry and Broder, 1966). These references suggest the range of studies which have been made although they are by no means a complete listing.

Through these and other publications on the spiny dogfish respiratory system, there runs a vein of vagueness as to the morphology of the gill and the relation of this to the physiological processes involved. For example, Burger and Bradley refer to branchial capillaries, but place quotation marks around the latter word without indicating the nature of the blood channels. Robin and Murdaugh (1967) in their chapter in "Sharks, Skates, and Rays" (page 222) refer to the "gill capillaries." Sheldon, Sheldon and Sheldon (1962) likewise refer to the capillaries of the lamellae. The present paper demonstrates that no capillaries are involved.

Other areas in which the morphology of the gill has special significance include the relatively small fall in blood pressure across the gill, the persistence of the pulse wave into the dorsal aorta, the means whereby large amounts of blood are accommodated, the muscular structure of the arteries, the possible presence of a countercurrent situation and the nature of the epithelium lining some of the water passages.

Materials and Methods

The basic method of investigation has been study of serially sectioned gills. Pieces from the approximate center of the gill were cut serially in one of three planes: (1) perpendicular to the surface of the gill and to the filaments (2) perpendicular to the surface of the gill, but parallel with the filaments; (3) parallel to

the surface of the gill and hence parallel with the filaments also. With gills of smaller fish complete serial sections were made from pieces of gill extending from the gill arch to the distal tips of the filaments, thus including a sample of the entire length of the filaments.

EXPLANATION OF LETTERING

BA	basal artery
BC	branchial chamber
CB	cavernous body
CR	cartilaginous ray
CTC	connective tissue core of filament
DA	distal artery
DS	dorso-lateral surface of body
FI	filament (primary lamella)
GS	gill slit
LN	large nerve
LS	lymph space
SE	septum (interbranchial)
SK	skin
SL	secondary lamella
SM	striated muscle
SN	small nerve
VS	ventro-lateral surface of body
WBC	wall of branchial chamber
WC	expanded water channel
WS	water space between filaments or between secondary lamellae

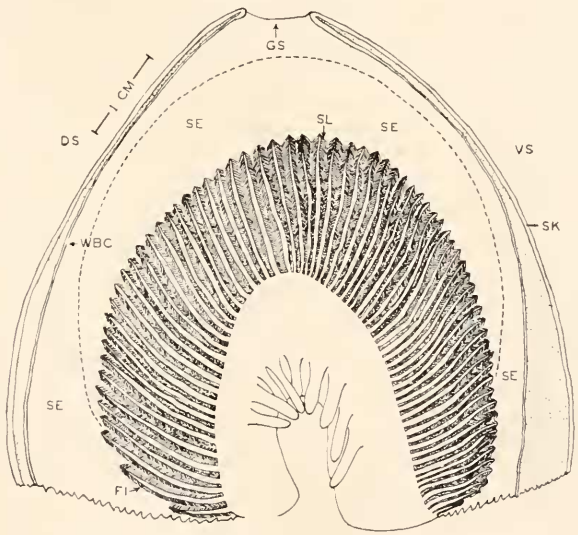

FIGURE 1. Face view of anterior hemibranch of gill number 4 (posterior hemibranch of gill pouch IV, considering the spiracle as pouch I). The broken line indicates the outer edge of the hemibranch on the posterior side of the septum. All microscope drawings made with the aid of projection, finer details being added free-hand during observation of the slide. For explanation of lettering in this and in all following figures see above.

The course of blood through the gill was followed by injecting dilute india ink into the ventricle and allowing 15 to 60 seconds to elapse before clamping the ventral aorta and removing the gill for fixation.

In general alternate slides of serial sections were stained with Delafield's haematoxylin and eosin, and with one or another version of Mallory's connective tissue stain. Some nerve impregnations were made and the material serially sectioned in the three different planes.

The Structure of the Gill

Gross structure

Each group of gill filaments is attached to one of the interbranchial septa separating gill pouches. Thus each gill pouch (except the most posterior) has part of a gill (a hemibranch) on both its anterior and posterior faces. However, a gill consists not of the two hemibranchs in one pouch, but the two which are attached to the opposite sides of the interbranchial septum. Unlike the situation in the teleosts the two hemibranchs of a gill are completely separated from one another, because the septum extends to the surface and is continuous with the skin.

Each hemibranch is composed of a number of ridges or filaments extending from the base of the gill toward its outer edge (Fig. 1). Due to the fact that the septum is not in the transverse plane of the body, but slants posteriorly as it extends outward, and the further fact that both hemibranchs end at approximately the same distance from the gill openings, it follows that the attachment of the hemibranchs is in a somewhat different position on the two sides of the septum (Fig. 1). When a section is made across the gill perpendicular to the filaments, those of the posterior hemibranch are cut closer to their proximal end. Since the filaments are arranged radially and become more separated as they pass distally, a given x-section through the gill will cut more filaments of the posterior than of the anterior hemibranch.

General topography

The general topography of the gill is illustrated in the stereogram (Fig. 2). This shows a portion of one gill, with the septum supporting six filaments on its anterior face and seven and a half on the posterior. The septum, supported by two elliptical cartilaginous rays, contains bundles of striated muscle fibers, two large nerves, and a considerable number of arteries which arise from the trematic branch of the afferent branchial artery. On the anterior face of the septum the arteries are arranged with a high degree of regularity; on the posterior face the presence of the cartilaginous rays interferes with the regular distribution of the arteries. The difference is due to the fact that the rays are not in the middle of the septum but are closer to the posterior surface.

Paralleling the arteries, and connecting with them at intervals, are somewhat rectangular structures which we shall term cavernous bodies (Dröscher, 1882). In one filament of the anterior hemibranch in Figure 2 the connection between the two structures is indicated. An artery and its accompanying cavernous body, extends to the very tip of each filament.

Between adjacent cavernous bodies is a water-filled space, bounded by an epithelium of large cells. This enlarged water passage continues the length of the filaments and is continuous also with water spaces between the secondary lamellae and between adjacent filaments. Typically there is a small nerve, containing eight to ten fibers, below the epithelium in the center of each large water passage.

The free surface of the filament is shaped like half a cylinder. Its outer covering is a thick epithelium, very richly supplied with mucous cells. This cap encloses a core of dense connective tissue within which are typically two cavities which appear to be lymph spaces and occasionally contain small clumps of red blood cells. It also includes a small nerve containing only six to eight fibers and an artery which

we shall call the distal artery. The last connects at the base of the gill with the collecting vessel of the efferent branchial artery. Each secondary lamella empties into a distal artery.

Connecting the distal mass of connective tissue with the wall of the cavernous body is a double sheet of connective tissue. In the space between these layers

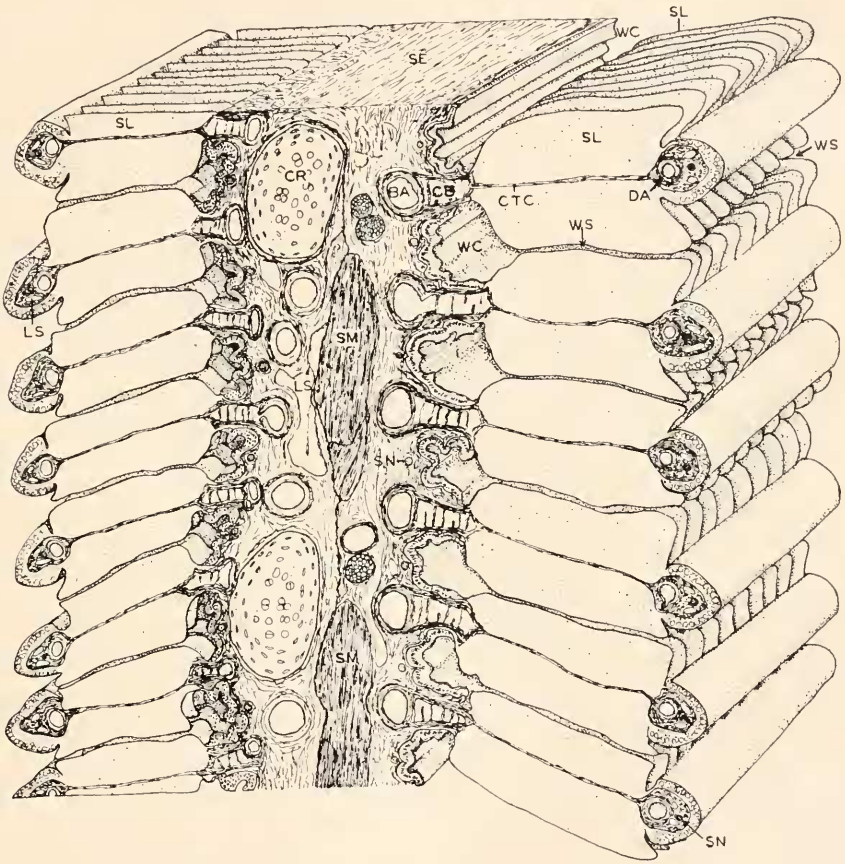

FIGURE 2. Stereogram of a portion of the gill. The front surface is a cross section through the gill perpendicular to the filaments. The anterior hemibranch is on the right, with parts of six filaments; the posterior hemibranch shows parts of eight filaments. The secondary lamellae are greatly simplified in this diagram. In actuality they are set at such an angle to the filaments that they appear in a cross section as they are seen in Figure 3.

there is an occasional red cell; the space also appears to be a pathway for nerves passing between the basal and distal parts of the filament. The drawing of these structures (Fig. 2) is based on a projection of a cross section of the gill, and is an accurate representation. However, the secondary lamellae are distorted greatly for the sake of clarity. They are attached along the connective tissue sheets in the center of the filament, and extend from the outer part of the cavernous body to the

distal artery. The distortion consists of representing these as being perpendicular to the septum and to the connective tissue layer. Actually they are set at angles.

The correct relationships appear in Figure 3, which is an accurate drawing of a cross section through one filament. Because of the angle at which the lamellae are attached, parts of seven are visible on each side. Red blood cells are omitted, and the space they occupied is represented by stippling for the sake of emphasis. The dark spots are accurate representations of flecks of ink resulting from a cardiac injection. The connection between the basal artery and the cavernous body is not seen, but there is a pair of connections between the cavernous body and secondary lamellae. The entrance of a secondary lamella into the distal artery is clear. The

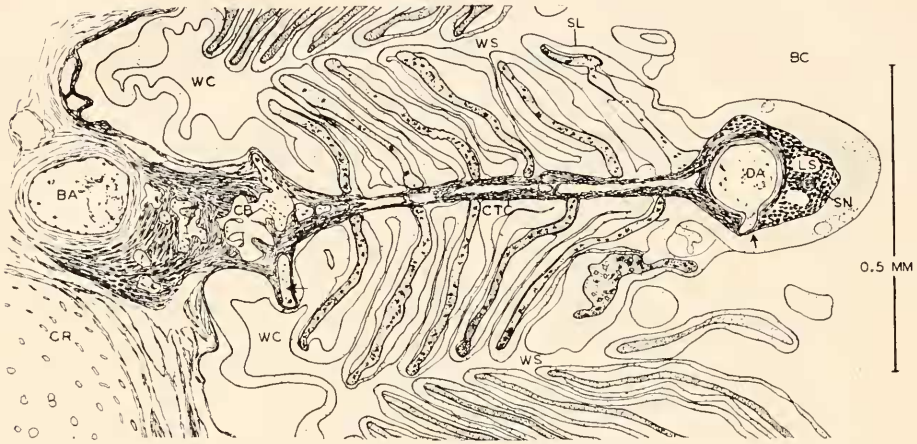

FIGURE 3. Cross section of filament from a posterior hemibranch. Red blood cells are omitted for clarity; the blood spaces are stippled more heavily than the epithelium, and contain flecks of ink injected into the heart. Arrows indicate connections between the secondary lamella and both the cavernous body and the distal artery.

space between the ends of the secondary lamellae of two adjacent filaments is shown, and the expanded water channels are indicated. The separation of the thick epithelium from the underlying tissue is an artifact.

The cavernous body

The cavity of the cavernous body appears to be divided into separate chambers by complete and incomplete partitions, when seen in sections perpendicular to the filaments (Fig. 4) or in sections parallel to the surface of the hemibranch. However, when examined in a section vertical to the surface but parallel to the filament, it is seen that these are not partitions but columns (Figs. 5 and 6). Each has a core to which large cells are attached, many of which contain pigment granules. While the number of granules is not very impressive in sections, they are present in sufficient number to impart a gray appearance to the entire organ when the gill is washed free of blood by the injection of saline. There is no indication of haemolysis of red cells as described by Acrivo (1935) in *Scyllium canicula*. The nature of the core is not entirely certain. In our preparations there is no reason to believe

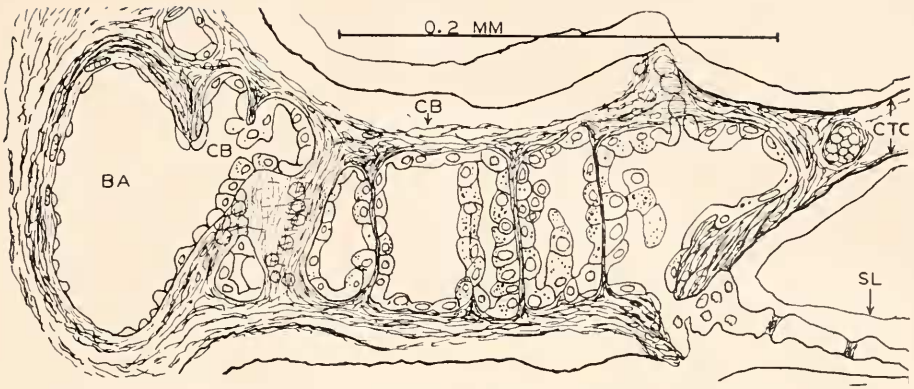

FIGURE 4. Basal artery and cavernous body. From a section perpendicular to the filament. Section is through opening between basal artery and cavernous body; and through the opening from the cavernous body to one secondary lamella. Pigment granules are placed accurately; red cells are omitted. Also omitted are cellular details of the epithelium which covers the secondary lamella and continues as the lining of the expanded water channel.

the core to be other than connective tissue. However, Sheldon, Sheldon and Sheldon (1962) described it as containing smooth muscle fibers.

The thick wall is composed mainly of a rather dense non-elastic connective tissue. This is continuous with the connective tissue surrounding the connecting artery,

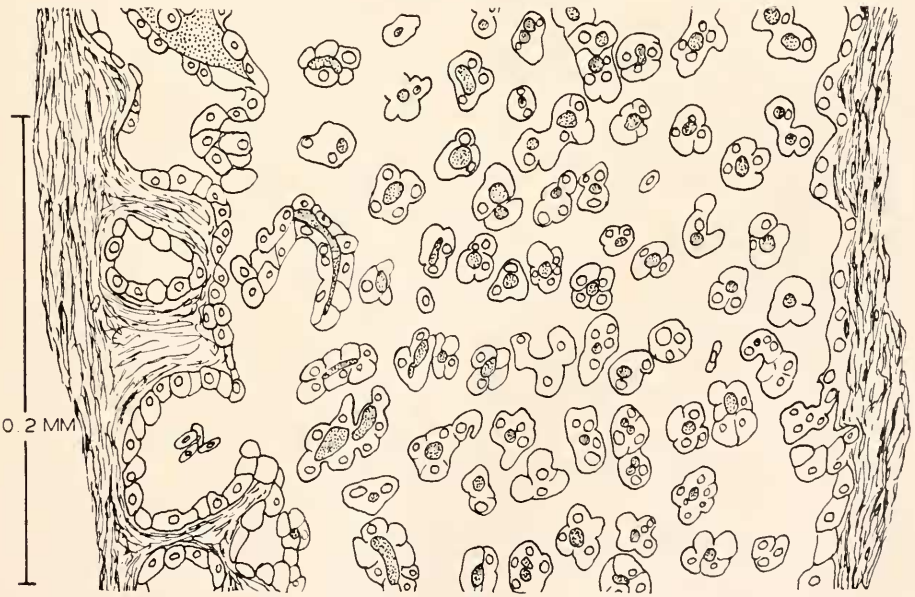

FIGURE 5. Columns of cavernous body. From a section perpendicular to the gill surface, parallel to the filaments. It is thus at right angles to the plane of section of Figures 2–4. Stippled area is the central core to which endothelial cells are attached; nuclei of the cells are shown as clear circles; pigment is not indicated. Openings on left are from basal arteries. Only a few red cells are included.

but the arterial muscle does not continue into the wall of the cavernous body. At the distal end of the cavernous body the wall is continuous with the double-layered sheet of connective tissue which forms the center of the filament. Figure 4 shows the exit from the cavernous body into a secondary lamella. The blood cells have been omitted for the sake of clarity, but all the blood spaces of the section were well

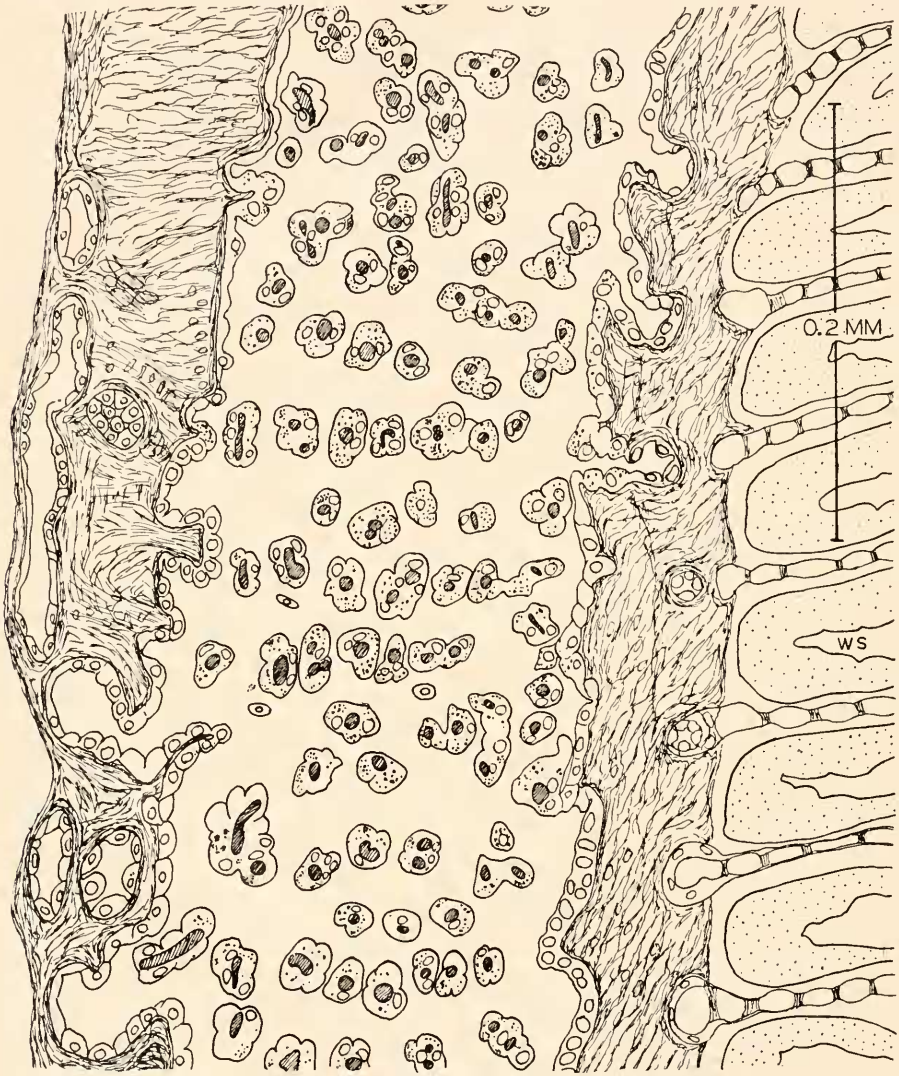

FIGURE 6. Columns of cavernous body. From a section perpendicular to the gill surface, parallel to the filaments. Central core of columns appears dark; pigment granules in endothelial cells are shown accurately. On left are openings into cavernous body from parallel artery; on right are openings from cavernous body into secondary lamellae. Epithelial layer is continuous with the surface of the lamellae and is indicated by stippling. Most of the red cells are omitted.

filled with erythrocytes. The connection to the other secondary lamella, lightly indicated here, appears two sections beyond this one.

The relationships are shown better in Figure 6. This is a drawing of a section parallel to the filament and perpendicular to the gill surface. Because the cut was made at a slight angle, there is a progression along the right wall. At the upper end is the exit from the lumen of the cavernous body; at the lower end is the entrance into the lamella proper. The space between the vascular channel and its overlying epithelia is present in all the sections but is presumed to be an artifact. The crypts and cavities of the opposite wall are connections between arteries and the cavity of the cavernous body. This becomes very clear when other sections of the series are examined.

From the scale which is included in the drawing it is clear that the number of secondary lamellae arising from the cavernous body can be considered to be approximately twenty pairs per millimeter. A similar value is reached when one counts the number of openings from arteries into the cavernous body.

The secondary lamellae

The lamellae, which were shown in Figure 5 taking their origin from the cavernous body, are thin structures which are shown diagrammatically in Figure 2, and as they actually appear in a cross section of a filament in Figure 3.

They are composed of a double sheet of epithelium which is seen well in Figure 7. This is a small part of the cross section through one lamella, the right end being the free edge of the sheet. In such a section the space between the epithelial layers, 0.01 to 0.02 mm in thickness, seems to be divided into a large number of channels containing red cells. It is these spaces which are referred to by many writers as capillaries. To be more accurate the apparent partitions are pilaster cells. Each seems to consist of a hollow tube with a fluted surface, composed of basement membrane which is continuous with that underlying the epithelium. The hollow tube contains the cell itself. This is compatible with the description of the ultrastructure of the teleost pilaster cells by Newstead (1967). The relationship is seen clearly in that part of the section where the epithelium is separated from its basement membrane. It also shows well in the bases of the secondary lamellae in Figure 6. Keys and Willmer (1932), in describing the pilaster cells of the eel, ascribed to them the function of keeping the two epithelial membranes apart, a concept which gave rise to their name. It would seem that their function is rather to hold the two epithelial layers together and prevent their being pushed apart by the pressure of the blood between them.

The essential difference between this arrangement and capillaries is seen more clearly from a different view. Figure 8 shows a section through a secondary lamella parallel to its surface. It is impossible to obtain more than a small part in a single section, due to its thinness. The upper right of the section is the distal artery, connected with the secondary lamella. One layer of epithelium is at the left, with the nuclei indicated; the other, cut at a long slant, is below with no cellular detail shown. The pilasters, now seen from their end, are stippled. A few red cells are included, but most of them are omitted for the sake of clarity. The distribution of pilasters is random, except near the outer edge of the lamella. Here they are somewhat enlarged and form a broken partition a short distance from

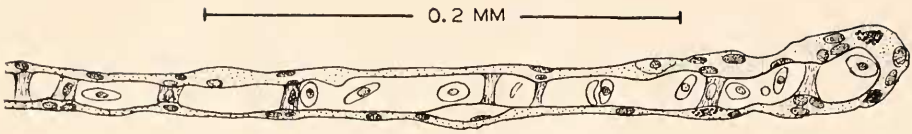

FIGURE 7. Structure of secondary lamella. Cross section through a secondary lamella near its free edge, which is at the right. The cavity is largest at the free edge. The apparent partitions are pilaster cells extending from one epithelium to the other.

the edge, a situation which results in the difference in appearance of the terminal space of a cross section of the lamella as seen in Figure 7. This is interpreted as a device which tends to spread the flow of blood more evenly across the cross-section area of the lamella.

The course of blood flow

From the information yielded by the injected animals, it is clear that the course of blood through the gills is as follows. Arising from the branches of the afferent branchial arteries, the basal artery carries the blood along the septum at the base of each filament, continuing to the very end of the filament. Along the outer surface of this artery there are approximately twenty openings per millimeter into the parallel cavernous body. Thus with a filament length of about 12 mm as shown in

FIGURE 8. Structure of secondary lamella. Section very nearly parallel to the surface of the lamella. The pilasters, seen in end view, are indicated by stippling with details omitted. A few of the red cells are included for comparison with the available spaces. The epithelium covering the lamella was cut at a slant; the outline of the nuclei is indicated in the upper epithelium.

Figure 1, there would be approximately 240 openings from each artery into its cavernous body. Any cell could pass through any one of them. Within the cavernous body, which also extends the length of the filament, blood has a considerable "choice" of direction of flow. A cell which had entered could be carried in either direction along its length, and there is considerable freedom of movement in other planes. Along each millimeter of the cavernous body there are approximately 20 pairs of exits, each exit opening into a secondary lamella. The latter is so thin that there

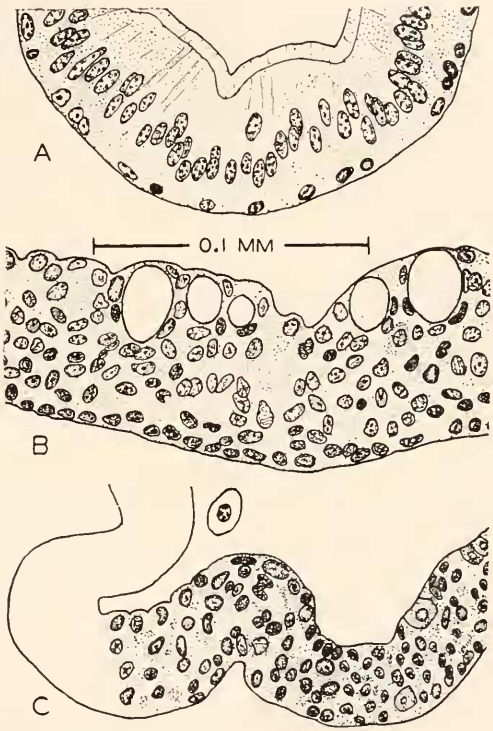

FIGURE 9. Epithelium of the expanded water channel. A. Small strip of the epithelium found in the basal half of the water channels of the anterior hemibranch. Outer surface of each cell is strikingly modified, either as a brush border or as cilia. B. Type of epithelium found in the distal half of the water channels of the anterior hemibranch. C. Type of epithelium found in all parts of the water channel of the posterior hemibranch. A brush border is never present. Mucous cells are also lacking.

is little room for movement except in one plane, but within that restriction blood is free to move in any direction. Finally twenty pairs of openings per millimeter lead into the distal artery from secondary lamellae. The distal artery in turn delivers the blood to the collector branch of the efferent branchial artery.

Water channels

It is clear that water bathes the epithelium which covers the lamellae. Water is thus located between the lamellae, and between the free edges of the lamellae of one

filament and those of the adjacent filament. Between the cavernous bodies the epithelium forms a wide-open channel, seen clearly in Figure 2. In the basal half of the anterior hemibranch the epithelium of this enlarged water channel is very regular, and the cells possess either a thick brush border or cilia (Fig. 9A). From our preparations one cannot decide which is present, but our interpretation leans toward a brush border. The distal half of the channel is quite different (Fig. 9B). The nuclei of the epithelium are randomly distributed, variable in size and staining capacity, and there are large numbers of mucous cells in different stages of development. Scattered larger cells with finely granular eosinophilic cytoplasm are interpreted as young mucous cells.

In the posterior hemibranch the corresponding spaces have a still different epithelium (Fig. 9C). There is never a brush border (or cilia); the epithelium is almost as thick but the nuclei are less regularly distributed, are more numerous, smaller and more deeply staining. There is an occasional larger eosinophilic cell with more lightly staining nucleus and clearly delimited finely granular cytoplasm. This type of epithelium lines the channel for its entire extent in the posterior hemibranch.

There is no information which demonstrates the course of water through these channels. We do not know the relative amounts which pass along the wide channel as compared with that between lamellae, or what fraction of the water passing through the gill pouch might move between the two hemibranchs without passing through any of the spaces indicated.

Discussion

Measurements of the difference in pressure between ventral and dorsal aortae show relatively little fall in pressure across the gills (Burger and Bradley, 1951). Fishman states (1967, page 216) that "Ingeniously, relatively little of this energy is lost as blood traverses the gills." The question arises how the blood can pass through the respiratory area without greater loss in pressure.

The morphological arrangements seem to offer a simple and clear explanation. It has been pointed out that blood from the basal artery is free to pass through many possible openings into the cavernous body; that within the cavernous body the blood is free to move in various directions and to exit through any one of many openings; that even within a lamella with its single entrance and exit, there is freedom of direction of movement among the pilaster cells. It is only when the blood has left the secondary lamella and has entered the distal artery that its flow again becomes restricted to one direction. With all this freedom of "choice" the blood will follow the course of least resistance. This is another way of saying that it will follow the line of least pressure drop, since the fall in pressure is due largely to overcoming resistance. Transient pile-ups of erythrocytes, which can be observed in the usual capillary circulation, may increase resistance to the point of markedly slowing or even stopping flow. In the blood channels of the gill such partial or complete blocking can have the effect only of diverting the flow to a course with less obstruction.

The arrangement of the blood in a sheet also results in a reduction of the area of contact between blood and wall, thus decreasing resistance. The area of contact in this arrangement is only about one half that which would prevail if the blood

were contained in parallel tubes of the same diameter and the same total cross-sectional area.

Sheldon, Sheldon and Sheldon (1962) were surprised that the pulse wave persisted as the blood passed through the gill. They called attention to what they named the "arterial sinus" and which we have termed the cavernous body. They comment that this should be "ideally suited to damp out any pulse wave." However, they appear to have considered that the passageways through the structure were more tortuous than they really are, and that the core of the "trabeculae" consisted of smooth muscle. Figure 6 shows that the course of blood is not necessarily tortuous. The outer wall appears to have little elasticity and the core of the columns is probably non-elastic connective tissue and not smooth muscle. Furthermore a considerable degree of rigidity of the lamellae must result from the presence of very large numbers of pilaster cells. These factors, taken together, give reason for the persistence of the pulse wave through the gill. Stretching and recoil of the containing walls are required to absorb and damp out the pulse wave.

Another question which arises is how such a large amount of blood can pass through the gills, since as much must pass through these as through the entire systemic circulation. In our preparations there is no evidence of shunts between the afferent and efferent supply of the gills, which is in agreement with the findings of Sheldon, Sheldon and Sheldon. This study does not give morphological support for the statement of Robin and Murdaugh (1967) that "there is indubitable evidence that there is some degree (usually small) of pregill to postgill shunting" (page 236). Piiper and Shumann (1967), working with the dogfish *Scyliorhinus stellaris,* accept the difference in gill arrangement in elasmobranchs and teleosts. But in spite of these differences they also accept the presence of shunts between basal and distal arteries of the filament because such shunts are reported in the teleosts by Steen and Kruysse (1964). If there are morphological shunts in Squalus they are probably in the basal part of the gill, proximal to the base of the filaments. This possibility was not investigated. Certainly most of the blood is distributed through relatively large vessels (basal arteries and cavernous bodies). Then suddenly the blood is delivered to perhaps 30,000 parallel lamellae in each hemibranch. With 18 hemibranchs, the total dispersion through parallel channels is of the order of half a million. The individual blood cell, however, travels only a millimeter or two in traversing the lamella. The abrupt beginning and end of the finer channels, and their parallel arrangement, are well suited to provide the structural mechanism for allowing large amounts of blood to pass through the gills.

The course of blood through the lamellae is clear. The question arises whether the structure furnishes the possibility of a counter-current flow relative to the water. The arrangement of the gill is very different from that of the teleosts in which the counter-current flow was first described by van Dam (1938) and supported by the experiments of Hazelhoff and Evenhuis (1952).

With the known route of blood, to give a complete counter-current it would be necessary for the water to move into the space between the outer ends of the lamellae, and then pass inward between adjacent lamellae to the enlarged water channel lying between cavernous bodies. It is possible that this is the route taken by the water, but without further evidence this must remain dubious. The structure of the gills seems to fit better the "multicapillary" model suggested by Piiper

and Schumann (1967). It becomes clear that more information is needed concerning the details of water flow. Robin and Murdaugh (1967) conclude on physiological grounds that the counter-current pattern does not fit their findings, and also that only 50% of the total inspired water seems to be effective in gas exchange. The various courses which water might follow may be of significance in relation to these findings.

One peculiarity which appears in our material is the fact that the diameter of the distal artery appears in sections to be markedly smaller than that of the basal artery. It is clear that all the blood entering through the basal artery must leave the filament through the distal one. It does not seem possible that the difference in diameters can exist to such a degree in the living state. This would cause a fall in the post-gill pressure greater than actually occurs. In distal arteries whose cross section is very small the thickness of the muscle layer is greater than that of the basal artery. However, when arteries of similar size are compared in the sections, the thickness of the muscle layer seems to be of the same order. While it could be argued that only those with the same amount of muscle show the same diameter in sections, it seems more probable that the different sizes in sections represent a difference in response to the process of fixation. It might mean only that the distal arteries are preserved in a more contracted state than the less accessible and more slowly fixed basal arteries. Satchell (1962) concluded that anoxia in *Squalus acanthias* causes a vasoconstriction at some point in the gills before the lamellae are reached. The basal arteries furnish a possible site. However, the potential contractility of the distal arteries must also be taken into consideration in the interpretation of vascular changes.

The presence of a well-formed brush border on the cells of the basal half of the water channels of the anterior hemibranch raises several questions and answers none. Why this should be found only in the basal half, and why there should be none in the posterior hemibranch, must at present remain unanswered. Available data do not furnish a clue to the function of these brush-border cells. The data on exchange between blood and sea water in this species demonstrate that a very impermeable membrane separates blood and water. For example, although the major part of the urea passing from the blood to the exterior does so through the gills rather than the kidneys (Smith, 1931; Goldstein and Forster, 1962) it must be remembered that the concentration gradient is extremely high, since the concentrations in blood and sea water are approximately 20 g/l and zero. In absolute values the gill membrane is nearly impermeable to urea. According to Boylan (1967), compared to the urinary bladder of the toad the gill is only $\frac{1}{12}$ to $\frac{1}{15}$ as permeable to water and sodium, and only $\frac{1}{35}$ as permeable to urea. While the rate of exchange of urea at the gill varies with temperature and deviation from normal blood levels, Boylan does not consider that the data indicate active transport of urea. In fact there is no conclusive evidence of active transport across this gill, despite the branchial elimination or absorption of many substances. For example, Horowicz and Burger (1968) found that the influx of sodium through the gills is of the same order as through the skin, but the greater surface of the gills gives a greater total influx by that route. Their data do not indicate whether there is active transport. There is little evidence at this time that presence of cells with a brush border is correlated with active transport across the gill.

Summary

1. The course of blood through the gills is described.

2. Blood passes first into arteries which parallel the filaments and lie at their base.

3. Blood then passes into the overlying parallel cavernous bodies through any of the approximately 20 openings per millimeter.

4. The cavernous bodies have non-elastic walls and, passing across the lumen, non-elastic columns. Blood is free to flow in any direction through the cavernous bodies. Each cavernous body has approximately 20 pairs of exits per millimeter, each one opening into a secondary lamella.

5. The secondary lamella does not contain capillaries, but consists of two sheets of epithelium held together, with a constant space between them, by large numbers of pilaster cells. Within the single plane of this structure blood is free to move in a variety of directions between its entrance and its exit into the distal artery.

6. Within the freedom of movement provided by the basal artery, cavernous body and secondary lamella, blood is free to follow the line of least resistance. This results in its following the line of least pressure fall, and accounts for the small loss of pressure during transit of the gill.

7. The cavernous body appears to be rather rigid, and the large number of pilaster cells restricts the separation of the two epithelial layers and must impart a degree of rigidity to the walls of the vascular spaces. It is due to the consequent restriction of stretch and recoil that the pulse wave is relatively undamped and continues into the dorsal aorta.

8. The arrangement of blood vessels into myriads of parallel sheets which start and end abruptly provides the anatomical basis by which large amounts of blood are passed through a seemingly highly restricted area.

9. There is evidence that both the basal and distal arteries have sufficient muscle tissue to be potentially capable of some degree of contractility, a factor which should be taken into consideration relative to vascular changes.

10. There is no apparent explanation for the presence, in the basal half of the water passages of the anterior hemibranch, of an epithelium with what appears to be a highly developed brush border.

11. The anatomical arrangement of the gill seems to fit a multicapillary model better than a counter-current one. However more information is needed as to the details of water flow in relation to vascular structures before a definite conclusion can be reached.

LITERATURE CITED

Acrivo, C., 1935. Sur l'organization et la structure du corps caverneux chez *Scyllium canicula* Cuv. *Bull. Histol. Appl. Physiol. Path.*, 12: 362–372.

Balabai, P., 1939. A study of the work of the respiratory apparatus in Selachians. *Acad. Sci. Ukr. S.S.R. Pap. Animal Morphol.*, 5: 73–110.

Bigelow, Henry B., and William C. Schroeder, 1948. Fishes of the Western North Atlantic. Part I: Lancelets, Cyclostomes, Sharks. *Memoir Number 1 of the Sears Foundation for Marine Research.* 576 pp.

Boylan, J. W., 1967. Gill Permeability in *Squalus acanthias*, pp. 197–206. *In:* P. W. Gilbert, R. F. Mathewson, and D. P. Rall, Eds., *Sharks, Skates, and Rays.* Johns Hopkins University Press, Baltimore, Maryland.

Boylan, J. W., R. Johnson and D. Antkowiak, 1962. Gill permeability in *Squalus acanthias*. *Bull. Mt. Desert Isl. Biol. Lab.*, 5(1) : 3.

Boylan, J. W., K. Kim, J. Farber and B. Gerstein, 1965. Osmoregulation in *Squalus acanthias* in hyperosmotic environment. *Bull. Mt. Desert Isl. Biol. Lab.*, 5(2) : 3.

Burger, J. Wendell, and Stanley E. Bradley, 1951. The general form of circulation in the dogfish, *Squalus acanthias*. *J. Cell. Comp. Physiol.*, 37: 389–402.

Burger, J. Wendell, and D. C. Tosteson, 1966. Sodium influx and efflux in the spiny dogfish, *Squalus acanthias*. *Comp. Biochem. Physiol.*, 19: 649–653.

Dröscher, Wilhelm, 1882. Beiträge zur Kenntnis der histologischen Struktur der Kiemen der Plagiostomen. *Arch. Naturgesch.*, 48: 120–177.

Fishman, Alfred P., 1967. Some Features of the Respiration and Circulation in the Dogfish, *Squalus acanthias*, pp. 215–219. *In:* P. W. Gilbert, R. F. Mathewson, D. R. Rall, Eds., *Sharks, Skates, and Rays*. Johns Hopkins University Press, Baltimore, Maryland.

Gilbert, Perry W., Robert F. Mathewson and David P. Rall, Editors, 1967. *Sharks, Skates, and Rays*. Johns Hopkins University Press, Baltimore, Maryland, 624 pp.

Goldstein, Leon, and Roy P. Forster, 1962. The relative importance of gills and kidneys in the excretion of ammonia and urea by the spiny dogfish (*Squalus acanthias*). *Bull. Mt. Desert. Isl. Biol. Lab.*, 4: 33.

Hazelhoff, E. H., and H. H. Evenhuis, 1952. Importance of the "counter-current principle" for the oxygen uptake in fishes. *Nature*, 169: 77.

Horowicz, P., and J. Wendell Burger, 1968. Unidirectional fluxes of sodium ions in the spiny dogfish, *Squalus acanthias*. *Amer. J. Physiol.*, 214: 635–642.

Keys, Ancel, and E. N. Willmer, 1932. "Chloride secreting cells" in the gills of fishes, with special reference to the common eel. *J. Physiol. (London)*, 76: 368–378.

Lenfant, C., and K. Johansen, 1966. Respiratory function in the elasmobranch, *Squalus suckleyi* G. *Resp. Physiol.*, 1: 13–29.

Maren, Thomas H., Rececca Embry and Lawrence E. Broder, 1966. Excretion of drugs across the gill of the dogfish, *Squalus acanthias*. *Bull. Mt. Desert Isl. Biol. Lab.*, 6: 25–28.

Murdaugh, H. Victor, Jr., and E. D. Robin, 1967. Acid-base Metabolism in the Dogfish Shark, pp. 249–264. *In:* P. W. Gilbert, R. F. Mathewson, D. P. Rall, Eds., *Sharks, Skates, and Rays*. Johns Hopkins University Press, Baltimore, Maryland.

Newstead, James D., 1967. Fine structure of the respiratory lamellae of teleostean gills. *Z. Zellforsch. Mikrosk. Anat.*, 79: 396–428.

Piiper, J., and D. Schumann, 1967. Efficiency of O_2 exchange in the gills of the dogfish, *Scyliorhinus stellaris*. *Resp. Physiol.*, 2: 135–148.

Rall, David P., Nicholas R. Bachur and Jeffery Ratner, 1966. The movement of foreign organic compounds across the gills of marine animals. *Bull. Mt. Desert Isl. Biol. Lab.*, 6: 31–32.

Robin, Eugene D., and H. Victor Murdaugh, Jr., 1967. Gill Gas Exchange in the Elasmobranch, *Squalus acanthias*. Chapter 15, pp. 221–247. *In:* P. W. Gilbert, R. F. Mathewson, D. P. Rall, Eds., *Sharks, Skates, and Rays*. Johns Hopkins University Press, Baltimore, Maryland.

Robin, Eugene D., Herschel V. Murdaugh, Jr. and J. Eugene Millen, 1966. Acid-base, fluid and electrolyte metabolism in the elasmobranch. III. Oxygen, CO_2, bicarbonate and lactate exchange across the gill. *J. Cell. Comp. Physiol.*, 67: 93–100.

Satchell, G. H., 1962. Intrinsic vasomotion in the dogfish gill. *J. Exp. Biol.*, 39: 503–512.

Sheldon, Warner F., Wendy Sheldon and Lura Sheldon, 1962. The pulse wave in *Squalus acanthias*. *Bull. Mt. Desert Isl. Biol. Lab.*, 4: 79.

Smith, Homer W., 1929. The excretion of ammonia and urea by the gills of fish. *J. Biol. Chem.*, 81: 727–742.

Smith, Homer W., 1931. The absorption and excretion of water and salts by elasmobranch fishes. II. Marine elasmobranchs. *Amer. J. Physiol.*, 98: 296–310.

Steen, Johan, and A. Kruysse, 1964. The respiratory function of teleostean gills. *Comp. Biochem. Physiol.*, 12: 127–142.

van Dam, Levie, 1938. On the utilization of oxygen and regulation of breathing in some aquatic animals. *Dissertation, Groningen University*.